Description of European *Chamaesphecia* spp. (Lepidoptera: Sesiidae) feeding on *Euphorbia* (Euphorbiaceae), and their potential for biological control of leafy spurge (*Euphorbia esula*) in North America

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Abstract

The description of the ten *Chamaesphecia* species associated with *Euphorbia* in eastern and south-eastern Europe is based on external adult morphology, male and female genitalia, and the structure of the egg chorion. These species can be divided into two groups according to the shape of the setae of the dorso-basal part of the valvae in the male genitalia. Most *Chamaesphecia* species are associated with one species of host-plant and all are closely tied to one habitat type. The host-plant and the structure of the egg chorion are fundamental characteristics for the determination of a few species, and very helpful for the others. All species bore into the main root of their host-plant and overwinter as larvae. With the exception of two species which have an annual or biennial life cycle, all species are univoltine. The larvae of three of the eight *Chamaesphecia* spp. investigated feed and develop in the roots of North American leafy spurge, *Euphorbia esula* sensu lato. Of these, the best candidate for the biological control of leafy spurge is *C. crassicornis*, because the larvae have a similar survival rate on the target weed and the European host-plant, *E. virgata*.

Introduction

Leafy spurge (*Euphorbia esula* Linnaeus *sensu lato*) (Crompton *et al.*, 1990) is a toxic deep-rooted herbaceous perennial of Eurasian origin that has become a serious problem in pastures, prairies and non-crop-land areas in North America. The weed has been recorded in 26 states in the USA (Dunn, 1979) and in all Canadian provinces excluding Newfoundland (Frankton & Mulligan, 1987). The economic losses for the Dakotas, Montana and Wyoming in 1990 were estimated at over $100 million (Anon., 1992) and could reach $144 million annually by 1995 (Bangsund & Leistritz, 1991). The application of herbicides is economically not justifiable in most of the low productivity and recreation areas infested by leafy spurge. The *E. esula* group of species in Europe is attacked by a large complex of specialized insects and pathogens, and thus it is a suitable target weed in North America for classical biological control (Gassmann & Schroeder, 1995).

Leafy spurge is quite variable morphologically and there is considerable controversy as to whether leafy spurge is a single variable species or an aggregate of two or more species (see Radcliff-Smith, 1985; Stahevitch *et al.*, 1988; Crompton *et al.*, 1990 and references therein). Furthermore, uncertainty remains about the relationship of North American leafy spurge to European taxa. Although Smith & Tutin (1968) demote *E. virgata* Waldst. & Kit to subspecific status within *E. esula*, most European botanists maintain *E. esula* and *E. virgata* as separate species. European populations show greater variability in the number of triterpenoids present in the latex than has been detected in North American accessions of leafy spurge (Holden & Mahlberg, 1992). In this paper, we follow the recommendation by Crompton *et al.* (1990) that North American leafy spurge

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should be named *E. esula* sensu lato. For European plants we discriminate between *E. esula* (sensu stricto) *and E. virgata* (=*E. esula* subsp. *tommasiniana* (Bertol.) Nyman) (Smith & Tutin, 1968).

A programme for the biological control of leafy spurge was started by the International Institute of Biological Control (IIBC, formerly CIBC) and Agriculture Canada in 1961. *Chamaesphecia empiformis* and *C. tenthrediniformis* (Lepidoptera: Sesiidae) were tentatively released in Canada in the early 1970s but failed to become established. (Gassmann & Schroeder, 1995). *Chamaesphecia crassicornis* received attention in the early 1980s (Pecora *et al.*, 1990). We carried out field surveys in eastern Europe between 1987 and 1990 with the aim of discovering and studying other potential *Chamaesphecia* spp. for biological control of North American leafy spurge.

The first part of this paper includes a diagnosis of ten *Chamaesphecia* species based on external adult morphology, male and female genitalia, and the structure of the egg chorion. An account is given on their ecology and biology. The second part assesses the potential of most species for the biological control of North American leafy spurge.

Materials and methods

Surveys were carried out between 1987 and 1990 in Hungary, Slovakia, Serbia and the western part of Romania. Mature larvae were collected from infested roots, and the roots kept vertically in plastic containers at about 25°C, and covered with a mixture of sand and perlite. Early emerging males were kept in small vials (2.5×6.5 cm) in a dark container at 11–13°C to reduce their activity and preserve their reproductive capability. The females were put into transparent plastic cylinders (15×11 cm) and exposed to natural daylight. Females were exposed to males only when the ejection of their ovipositor indicated that they were ready for mating, generally within 24 h of emergence. One or two males were exposed to each female. Copulation occurred usually within 10 min. Mating containers were changed after each copulation or appropriately cleaned to avoid confusion from remaining pheromones. Oviposition was obtained on 15 cm long cut shoots inserted in pots filled with perlite and covered with a plastic cylinder. Ovipositing females were fed with a few drops of a sugar–honey solution. Potential fecundity was estimated by dissection of the females.

The suitability of leafy spurge from Saskatchewan (Canada) and Montana (USA) was tested and the European field host-plants used as controls. A replicate usually consisted of five newly hatched larvae which were transferred onto the shoot base of one potted plant. The plants were kept in the laboratory for 2–3 days before their transfer to a greenhouse. The plants were dissected at the end of October.

Description of *Chamaesphecia* species with notes on their ecology and biology

Sesiidae is a cosmopolitan family of 1063 described species (Heppner & Duckworth, 1981). Morphologically it is a well defined group of insects with transparent wings and bright coloured rings on the abdomen, mimicking wasps and bees (for a detailed account on the morphology of the Sesiidae, see Naumann, 1971; Fibiger & Kristensen, 1974).

The genus *Chamaesphecia* Spuler, is restricted to the western and central Palaearctic Region and comprises 82 species (Lastuvka, 1988; Spatenka *et al.*, 1993), but recently a new species was described from the eastern Palaearctic (Tosevski, 1993). No species of Sesiidae has been recorded on native North American spurge species (Eichlin & Duckworth, 1988). Lastuvka (1988) recognized two subgenera within the genus *Chamaesphecia* according to the morphology of the male genitalia and the host plant of the moth; the subgenus *Chamaesphecia* (sensu stricto) which is associated with *Euphorbia* species, and the subgenus *Scopulosphecia* associated with plant species in the families Lamiaceae, Scrophulariaceae and Hypericaceae. Twenty three of the 82 Palaearctic *Chamaesphecia* species are associated with *Euphorbia* species. Most *Chamaesphecia* species for which host plants are known are associated with only one plant species or with a few very closely related plant species. The need for further work on the taxonomy of European *Chamaesphecia* species was highlighted when *C. empiformis* and *C. tenthrediniformis* were recognized as two sympatric species on the basis of their life history, host-plants and structure of the egg chorion (Naumann & Schroeder, 1980). Previous work on *Chamaesphecia* species associated with *Euphorbia* species in Europe has been summarized by Naumann & Schroeder (1980) and Lastuvka (1982). Ten *Chamaesphecia* species, nine host-plant species and 88 sites were covered by our surveys in eastern and south-eastern Europe.

Chamaesphecia tenthrediniformis (Denis & Schiffermüller)

(figs 1–4, 30, 39–41)

Sphinx tenthrediniformis Denis & Schiffermüller, 1775: 44.
Sesia taediiformis Freyer, 1836: 142 (syn.).

Diagnosis. Alar expanse 15–22 mm. Fore wing black, with well developed hyaline areas in male, posterior transparent area (PTA) in female usually reduced. Discal spot black, exterior transparent area (ETA) field oval, divided into five cells. Apical area black between veins, with golden-yellow spots. Abdomen black, posterior margin of 2nd, 4th and 6th (and 7th for male) tergite golden-yellow, along medial abdominal line with more or less distinct golden-yellow pattern. Anal tuft black, in male with golden-yellow stripe medially, in female with individual yellow scales. The male and female genitalia are represented in figs 1–4, 30.

Egg structure. Eggs small (0.61 ± 0.03×0.41 ± 0.02 mm, n=30), pale brown-yellow, micropylar end flattened, rosette with micropyle clearly visible (figs 39–41). Average number of aeropyles 72.5 ± 12.4 (n=15, range 40–93).

Distribution and habitat. Central, eastern and south-eastern Europe. Also recorded in Ukraine, southern Russia and Kazakhstan. Mesic to slightly moist habitats. On pastures, roadsides, embankments, canal banks, west-facing open habitats. Abundant at all sites surveyed.

Bionomics. Species univoltine. Host-plants are *E. esula* sensu stricto and *E. salicifolia* Host. The flight period extends from mid April to the end of June. The peak of the flight period of *C. tenthrediniformis* ex *E. esula* (sensu stricto) occurs in May. In contrast, adults emerging from *E. salicifolia* appear only in June. Oviposition occurs on the basal part of the flowering shoots, very rarely on younger

plants. Eggs are laid singly or in small groups. Up to 40 eggs can be laid per shoot but no more than three larvae have been found in the same plant. The larvae penetrate the plant at the root crown level and quickly bore down into the root. Almost all larvae reach the last instar (L6–L7) in late autumn and prepare an exit hole before hibernation. The larvae pupate inside the tunnels the following spring.

Laboratory rearing. Copulation takes place in the afternoon. Females laid on average 87 eggs (range 34–167, n=7). Potential fecundity was 199 eggs (range 178–214, n=7).

Chamaesphecia empiformis (Esper)

(figs 5–7, 31, 42, 43)

Sphinx empiformis Esper, 1783: 215.
Sphinx bombiciformis Geoffroy, 1785: 252 (syn.).
Sphinx empinaeformis Walker, 1856: 33 (syn.).

Diagnosis. Alar expanse 15–22 mm. Fore wing of males black with distinct transparent areas, anterior transparent area (ATA) and PTA of females strongly reduced. Discal spot black, ETA oval shaped, divided into 5 cells, often 4 in female. Apical area black with lemon-yellow spots between veins. Abdomen black, posterior margin of 2nd, 4th and 6th (for male also 7th) tergite lemon-yellow. All tergites more or less diffusely covered with yellow scales forming merging transverse stripes. Anal tuft rectangular, with yellow stripes medially and yellow scales laterally; female with anal tuft black richly mixed with yellow scales. The male and female genitalia are represented in figs 5–7, 31.

Egg structure. Eggs dark brown ($0.74 \pm 0.02 \times 0.51 \pm 0.02$ mm; n=30), micropylar end broadly flattened, rosette with micropyle clearly visible (figs 42, 43). Average number of aeropyles 31.0 ± 10.0 (n=15, range 17–73).
Note: a detailed description of the larva of *C. empiformis* (misidentified as *C. tenthrediniformis*) was given by Lastuvka (1982).

Distribution and habitat. Widely distributed in Europe, and across southern Russia to eastern Kazakhstan. *Chamaesphecia empiformis* is a common species in central and south-eastern Europe. In well-exposed dry to very dry habitats, with sandy and coarse soils.

Bionomics. Species univoltine. The host-plant is *E. cyparissias* Linnaeus. The flight period extends from mid May to the beginning of August. Females oviposit on the vegetative shoots of fertile plants, rarely on young plants. The eggs are laid singly on the lower leaf surface along the upper part of the plant. Several eggs are laid per plant. Newly hatched larvae penetrate the plant at the upper third of the stem, mine upwards then turn and mine down the stem into the roots. The larvae overwinter in the lower part of the root. Early in spring, the larvae build an exit canal and pupate in the upper part of the tunnel which is strengthened with layers of silk and scraps.

Laboratory rearing. Copulation and oviposition in captivity were difficult to achieve. Copulation occurs in the morning and in the afternoon. Eight females laid on average 18 eggs (range 0–28). Potential fecundity was 114 eggs (range 104–124).

Chamaesphecia astatiformis (Herrich-Schäffer)

(figs 8–10, 32, 44–46)

Sesia astatiformis Herrich-Schäffer, 1846: 70.
Sesia thyreiformis Herrich-Schäffer, 1846: 72 (syn.).
Sesia agathiformis Walker, 1856: 34 (syn.).

Diagnosis. Alar expanse 13–20 mm. Fore wing black, abundantly covered with yellowish scales. Hyaline areas well developed in male; ATA very reduced and PTA entirely covered with black scales in female. Discal spot black, ETA in male elongated oval, divided into 5 cells, front cell nearly covered with yellow scales, ETA small in female, oval, divided into 3–4 cells. Apical area in male black, wide, more or less pointed toward apex, with large yellow spots between veins. Apical area black in female, with faint yellow spots. Abdomen black, posterior margins of 2nd, 4th and 6th tergite white. Abdomen of male more or less intensively covered with pale yellow scales. Anal tuft black, with yellow medial stripes. In contrast to *C. tenthrediniformis*, the white margins of female tergites are clearly defined but the pattern of the tergites is less noticeable. The anal tuft is black. The species is variable in size and colour, with sexual dimorphism in the morphology of the wings and in the intensity of the colour of the abdomen. Sometimes, especially in the females, the abdomen is entirely black, with no white rings. The male and female genitalia are represented in figs 8–10, 32. Females of *C. astatiformis*, *C. tenthrediniformis* and *C. empiformis* are morphologically not clearly distinguishable in the adult stage, and the exact diagnosis can only be established by their egg chorions.

Egg structure. Eggs pear-shaped, reddish-brown to dark brown, with a pruinose surface ($0.68 \pm 0.04 \times 0.45 \pm 0.03$ mm, n=90). The surface of the chorion is characterized by deep furrows densely divided into irregularly featured areas giving it a sponge-like appearance. Micropylar end crater-like, covered with catkin-like protrusions obscuring the rosette (figs 44–46). The number of aeropyles, which are difficult to see, is 2–4.

Distribution and habitat. Eastern and south-eastern Europe. Recorded in Turkey, southern Russia and Central Asia. Mesic to dry loamy habitats, also on poorer soils where spurge is intermixed with a dense and high vegetation. On road sides, ruderal areas and along field margins. The species is adapted to a continental or subcontinental climate with warm summers. Because it does not occur on *E. salicifolia*, the ecological range of *C. astatiformis* is slightly narrower than that of *C. tenthrediniformis* and does not include sites with more humid conditions. The species is relatively common.

Bionomics. Species univoltine. The host-plant is *E. esula* sensu stricto. The flight period extends from early May to the end of June, thus occurring later than that of *C. tenthrediniformis* which lives on the same host-plant. Females oviposit on vegetative shoots, mostly on young plants. Eggs are laid singly on the lower leaf surface or in the leaf axil on the upper part of the plant. Competition between the larvae of *C. tenthrediniformis* and *C. astatiformis* is reduced by the preferences of females for different phenological stages of the host-plant. Competitive displacement on larger plants might be the reason for preference of *C. astatiformis* for small vegetative plants on which *C. tenthrediniformis* rarely oviposits.

Laboratory rearing. Copulation occurs late in the afternoon. Females laid on average 92 eggs (range 53–144, n=7). Potential fecundity was 151 eggs (range 67–252, n=7).

Chamaesphecia hungarica (Tomala)

(figs 11–13, 33)

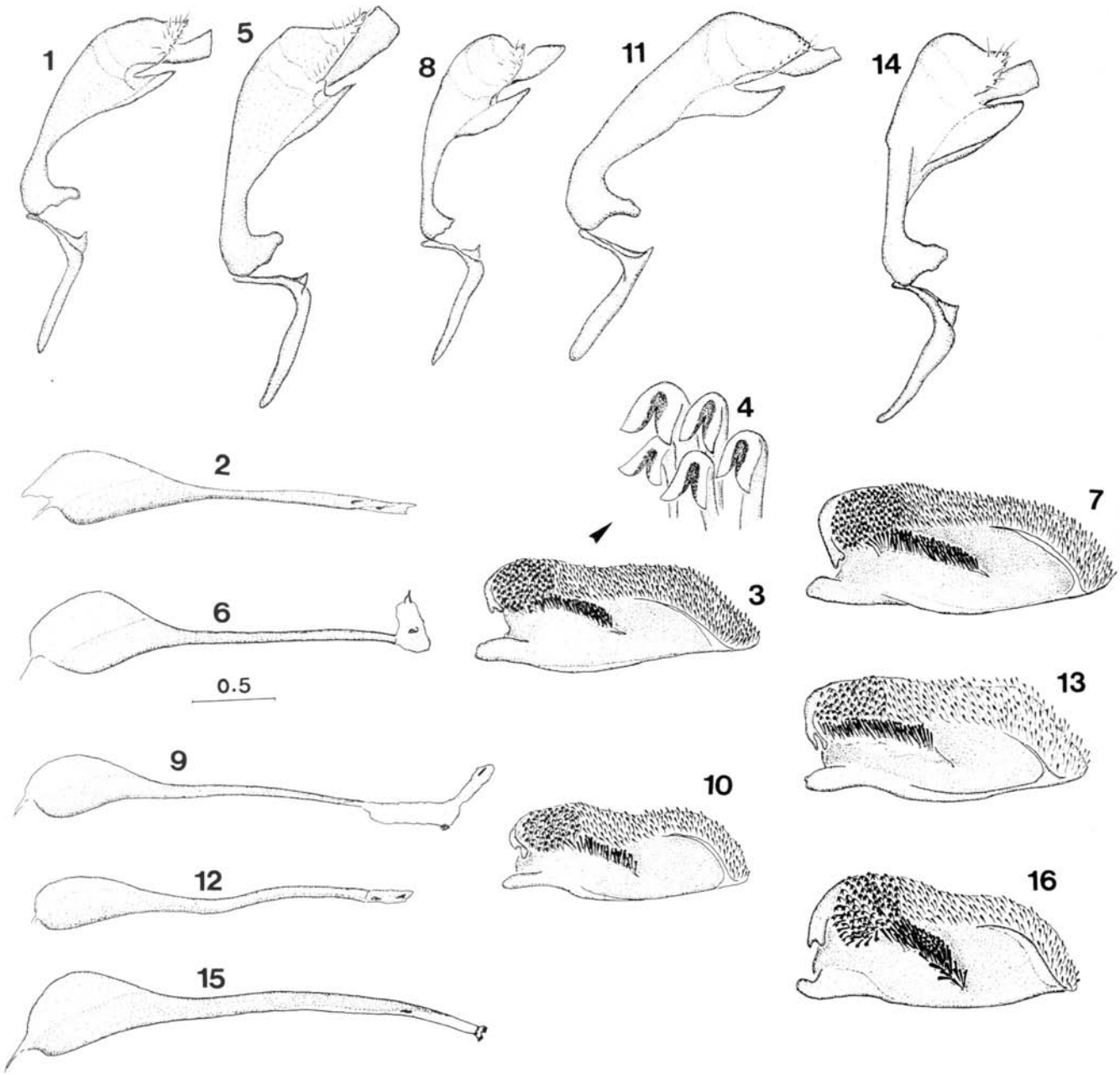
Sesia empiformis v. *hungarica* Tomala, 1910: 47.
Chamaesphecia deltaica Popescu-Gorj & Capuse, 1965: 341 (syn.).

Diagnosis. Alar expanse 15–21 mm. Fore wing black, male with all three hyaline areas distinct, female with PTA reduced to narrow stripes in the inner half. Discal spot black, ETA ovally shaped divided into 5 cells. Apical area black, with pale yellow spots between the veins. Abdomen black, posterior margins of 2nd, 4th and 6th (in male also 7th) tergite white, all tergites diffusely covered with yellowish scales with greenish iridescence. Anal tuft of male black, deltoid, with yellow stripe medially. Anal tuft of female black with abundant yellow scales. The male and female genitalia are represented in figs 11–13, 33.

Egg structure. Eggs dark brown (0.87 ± 0.09×0.53 ± 0.02 mm, n=30), micropylar end broadly flattened, rosette and micropyle clearly visible. Average number of aeropyles 49.0 ± 17.2 (n=15, range 20–97).

Note: a detailed description of the larva of *C. hungarica* is given by Lastuvka (1982).

Distribution and habitat. Eastern and south-eastern Europe. Common and locally abundant in Hungary and Serbia. Also recorded in south-western Ukraine. Swampy areas, river banks, ditches,

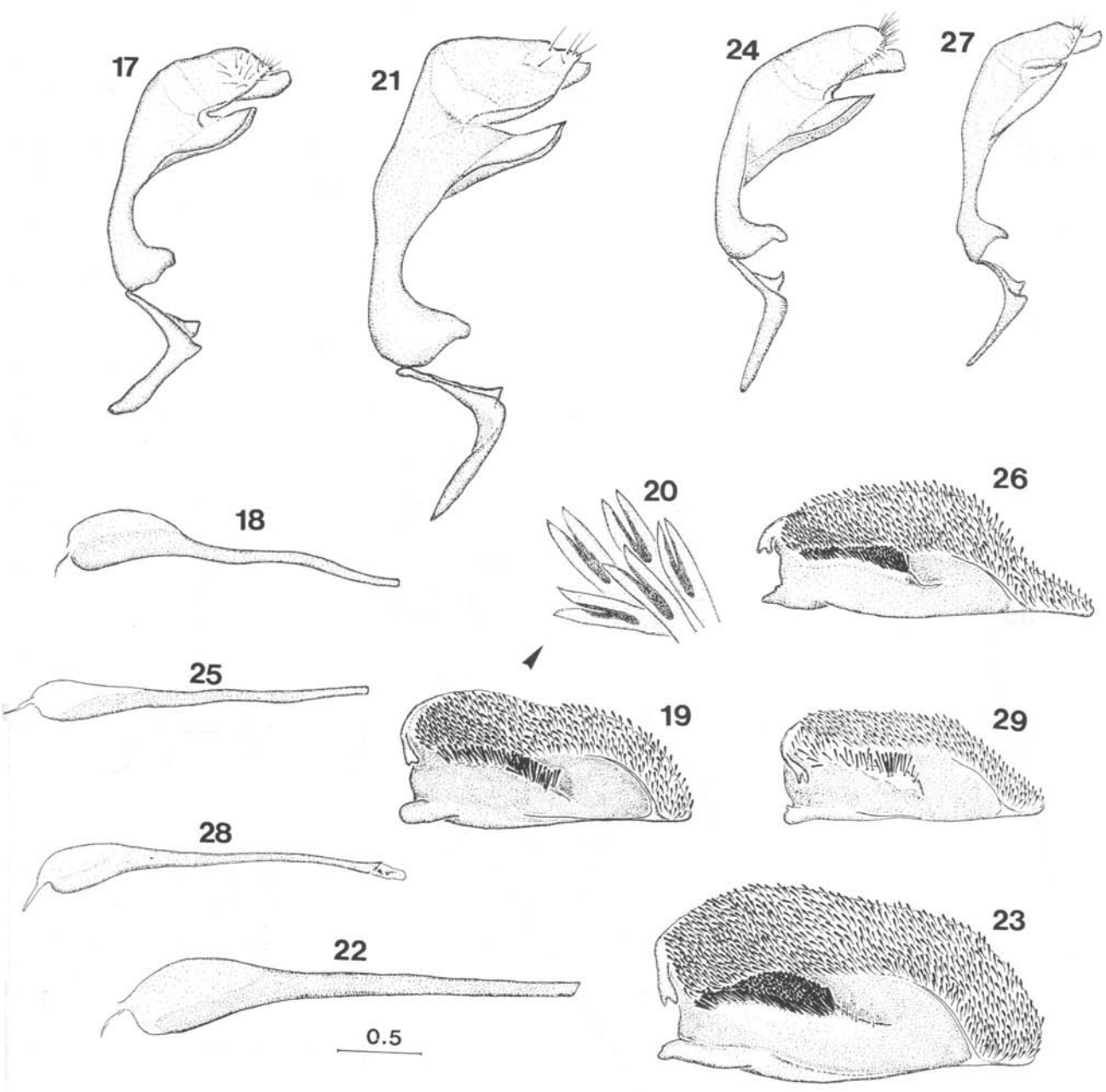


Figs 1–16, *tenthrediniformis*-group: male genitalia. Figs 1–4, *Chamaesphecia tenthrediniformis*: 1, uncus-tegumen complex; 2, aedeagus; 3, valva; 4, setae. Figs 5–7, *C. empiformis*: 5, uncus-tegumen complex; 6, aedeagus; 7, valva. Figs 8–10, *C. astatiformis*: 8, uncus-tegumen complex; 9, aedeagus; 10, valva. Figs 11–13, *C. hungarica*: 11, uncus-tegumen complex; 12, aedeagus; 13, valva. Figs 14–16, *C. bibioniformis*: 14, uncus-tegumen complex; 15, aedeagus; 16, valva.

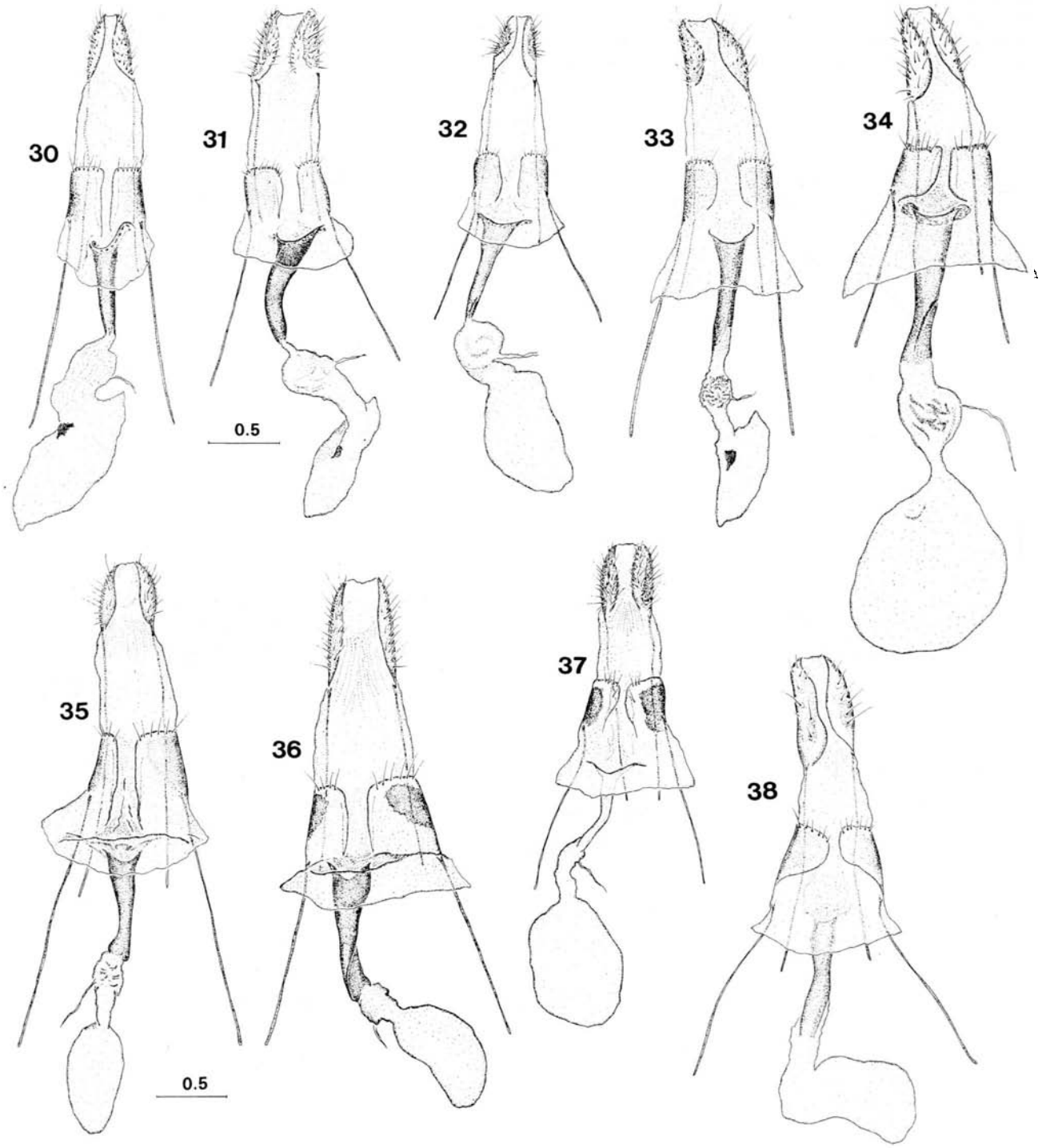
moist loamy and partly shaded sites. The species is adapted to a continental or subcontinental climate with warm summers.

Bionomics. Species univoltine. The host-plant is *E. lucida* Waldst. & Kit. The flight period extends from mid-May to mid-July. The eggs are laid singly or in small batches (up to 12 eggs) on the stem, the upper leaf surface and the inflorescence. Larvae penetrate into the host at the lower part of the shoot but most larval feeding occurs in the root. Larval development is completed in late autumn. Larvae overwinter in the lower part of the root, and in spring, the larva bores upwards, prepares an exit canal within the dry stem base and chews an emergence hole a few centimetres above the ground. Pupation occurs within the stem. There is no cocoon. The empty pupal exuviae is left protruding from the stem after emergence.

Laboratory rearing. Chamaesphecia hungarica copulates in the morning immediately after eclosion. Females laid on average 122 eggs (range 50–175, n=10). Potential fecundity was 202 eggs (range 182–214, n=10).



Figs 17–29, *euceraeformis*-group: male genitalia. Figs 17–20, *C. euceraeformis*: 17, uncus-tegumen complex; 18, aedeagus; 19, valva; 20, setae. Figs 21–23, *C. palustris*: 21, uncus-tegumen complex; 22, aedeagus; 23, valva. Figs 24–26, *C. leucopsiformis*: 24, uncus-tegumen complex; 25, aedeagus; 26, valva. Figs 27–29, *C. crassicornis*: 27, uncus-tegumen complex; 28, aedeagus; 29, valva.



Figs 30–38. Figs 30–34, *tenthrediniformis*-group, female genitalia: 30, *Chamaesphecia tenthrediniformis*; 31, *C. empiformis*; 32, *C. astatiformis*; 33, *C. hungarica*; 34, *C. bibioniformis*. Figs 35–38, *euceraeformis*-group, female genitalia: 35, *C. euceraeformis*; 36, *C. palustris*; 37, *C. leucopsiformis*; 38, *C. crassicornis*.

Chamaesphecia bibioniformis (Esper)

(figs 14–16, 34, 47, 48)

Sphinx bibioniformis Esper, 1800: 30.
Sesia tenthrediniformis v. *tengyraeformis* Boisduval, 1840: 42 (syn.).
Sesia empiformis v. *monspeliensis* Staudinger, 1856: 223 (syn.).

Diagnosis. Alar expanse 14–22 mm. All three transparent areas of wing well developed. Discal spot black, ETA area elongated oval, in female smaller, round, divided into 5 cells (in male usually 4 cells). Coxae of fore leg white. Abdomen black, posterior margins of 2nd, 4th and 6th (in male also 7th) tergite white. All tergites more or less ochre-yellow medially. Anal tuft black with light white stripe medially, in female with individual yellowish scales caudally. All posterior margins of the abdominal sternites whitish-yellow. The male and female genitalia are represented in figs 14–16, 34.

Egg structure. Eggs ashen black ($0.79 \pm 0.04 \times 0.58 \pm 0.03$ mm, n=30), micropylar end broadly flattened, rosette and micropyle clearly visible (figs 47, 48). Average number of aeropyles 53.3 ± 21.1 (n=15, range 20–115).

Distribution and habitat. Eastern, south-eastern and southern Europe. Recorded in southern Russia east to the Volga and Ural, and in southern Caucasus and Asia Minor. Sandy, dry to very dry well-exposed habitats. The species is adapted to both sub-mediterranean and continental climates and needs warm summers.

Bionomics. Species univoltine. The host-plant is *E. seguieriana* Necker but *C. bibioniformis* can also be found on other *Euphorbia* species, e.g. *E. nicaeensis* All. and *E. serrata* L., in southern Spain and the Middle East. The flight period extends from mid-May to the beginning of August. Females oviposit on the upper leaf surface of vegetative shoots. Newly hatched larvae penetrate the plant at the stem base and bore into the root. Up to 12 larvae have been found in a single root. Tunnels are usually straight and vertical within roots. There are seven larval instars and the larvae usually hibernate as 5th or 6th instar. In early spring, larvae bore up into the root crown and prepare a relatively long exit canal ending with a small tube of frass. Pupation occurs in the canal which is lined with numerous layers of silk.

Laboratory rearing. Chamaesphecia bibioniformis is a difficult species to breed in captivity. The percentage of successful mating was low (15%, n=20 pairs), and females laid only 17 eggs on average (range 0–110, n=20). Potential fecundity was 254 eggs (range 216–298, n=12).

Chamaesphecia myrsinites Pinker

Chamaesphecia myrsinites Pinker, 1954: 182.

Diagnosis. Chamaesphecia myrsinites looks like *C. bibioniformis*, but it is larger and more robust. The alar expanse is 22–28 mm. Fore leg with coxae brown-yellow to golden-yellow. Abdomen black, diffusely covered with golden-yellow, posterior margins of 2nd, 4th and 6th (in male also 7th) tergite white.

Egg structure. Eggs black with pale grey coating ($0.85 \pm 0.02 \times 0.617 \pm 0.02$ mm, n=30). Micropylar end widely flattened. Rosette and micropyle clearly visible. Average number of aeropyles 61.7 ± 27.6 (n=15, range 16–145).

Distribution and habitat. A rare species in south-eastern Europe. Occurs in well exposed dry to very dry habitats.

Bionomics. Species univoltine. The host-plant is *E. myrsinites* L. Like those of *C. bibioniformis*, the females of *C. myrsinites* oviposit on the upper leaf surface on the top of vegetative shoots. The oviposition behaviour and morphology of the adults suggest that *C. bibioniformis* and *C. myrsinites* might be one single species. However, if this is the case, host races might be present since selective oviposition has been observed at sites where both *E. seguieriana* and *E. myrsinites* were present.

Laboratory rearing. No copulation occurred in captivity from five males and nine females reared from field collected material.

Chamaesphecia euceraeformis (Ochsenheimer)

(figs 17–20, 35, 49–51)

Sesia euceraeformis Ochsenheimer, 1816: 171.
Sesia stelidiformis Freyer, 1836: 141 (syn.).
Sesia unicincta Herrich-Schäffer, 1851: Pl. 10., fig. 57 (syn.).
Chamaesphecia stelidiformis f. *amygdaloidis* Schleppnik, 1933: 24 (f.n.); Malicky, 1968: 96 (bionomy).

Diagnosis. Alar expanse 18–22 mm. Fore wing black, ATA reduced, PTA gradually covered with black scales. Distal spot black, ETA oval, divided into 5 cells. Apical area black between veins with golden yellow spots. Abdomen black, 1st tergite white laterally, posterior margin of 4th tergite broadly white. Broken golden-yellow stripe along medial line of abdomen. Anal tuft black, in male with golden-yellow stripe medially. The male and female genitalia are represented in figs 17–20, 35.

Egg structure. Eggs dark brown ($0.76 \pm 0.04 \times 0.47 \pm 0.03$ mm; n=30), micropylar end broadly flattened, rosette and micropyle clearly visible (figs 49–51). Average number of aeropyles 20.1 ± 5.8 (n=15, range 10–30).

Distribution and habitat. Central and southern Europe. Also known in southern Russia and northern Caucasus. Mesic loamy habitats. Open forests and forest margins. Locally abundant.

Bionomics. The host-plant is *E. polychroma* A. Kerner. Larval development is completed within one or two years. The flight period extends from June to the first half of July. Females oviposit either on the stems or the leaf axils of older plants. Larvae bore into the roots, making irregularly shaped tunnels. In early spring, larvae prepare an exit canal and pupate in the upper part of the tunnel in a cocoon-like chamber. Malicky (1968) found that *E. austriaca* A. Kerner is a host-plant of *C. euceraeformis* ssp. *amygdaloidis*. The taxonomic position of this subspecies is still unclear.

Laboratory rearing. Mating occurred in the morning. Females laid on average 82.8 eggs (range 68–108, n=6). Potential fecundity was 89.0 eggs (range 78–113, n=6).

Chamaesphecia palustris Kautz

(figs 21–23, 36)

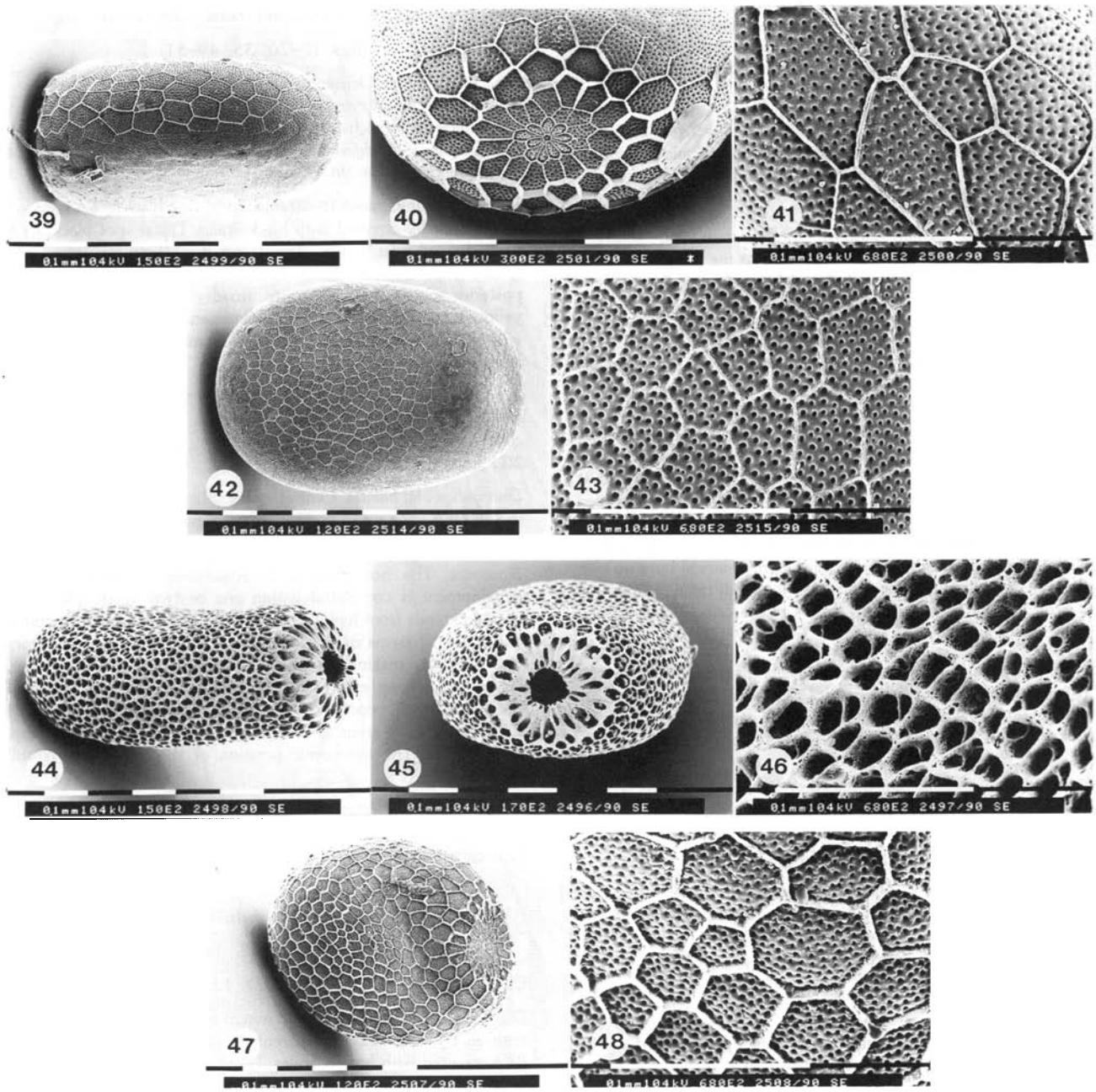
Chamaesphecia palustris Kautz, 1927: 12.

Diagnosis. Alar expanse 27–30 mm. Fore wing brown, in male with all hyaline areas transparent, in female ATA reduced, and PTA covered with brown scales. Discal spot dark brown, ETA in male widely oval, divided into 5 cells, ETA in female smaller and narrower, divided into 3–4 cells. Apical field brown. Abdomen brown, posterior margin of 4th tergite ochre-white. The male and female genitalia are represented in figs 21–23, 36.

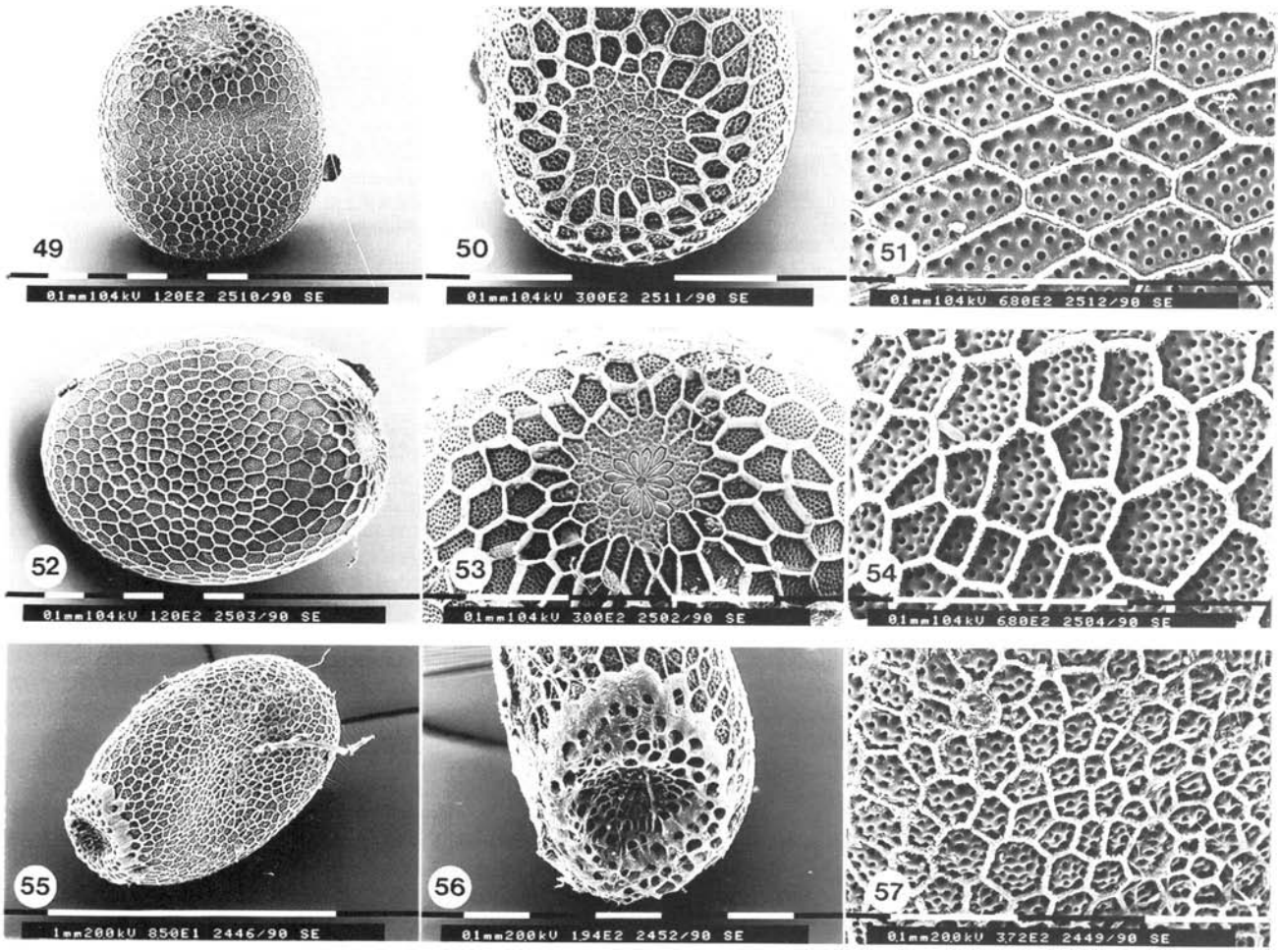
Egg structure. Eggs brown with a pale grey coating (1.06 ± 0.03×0.70 ± 0.02, n=30), micropylar end broadly flattened, rosette and micropyle clearly visible. Average number of aeropyles 18.7 ± 7.3 (n=60, range 8–30).

Distribution and habitat. Eastern and south-eastern Europe. Also known in Italy. Recorded in northern Turkey and Kazakhstan. Mesophile and swampy areas with compact soils, river banks and ditches.

Bionomics. Species univoltine. The host-plant is *E. palustris* L. The flight period extends from the end of May to the end of June. Eggs are laid in small batches on the dry stems. Larvae make irregular tunnels in the root. In early autumn, the larva makes a long tunnel (up to 40 cm) throughout the shoot and an exit hole high above the ground, a good adaptation to temporarily flooded sites. Larvae overwinter inside the root and pupate in the shoot the following spring. There is no cocoon.



Figs 39–48, *tenthrediniformis*-group: egg structure. Figs 39–41, *Chamaesphecia tenthrediniformis*: 39, overall view; 40, rosette; 41, enlarged view of the chorion. Figs 42–43, *C. empiformis*: 42, overall view; 43, enlarged view of the chorion. Figs 44–46, *C. astatiformis*: 44, overall view; 45, rosette; 46, enlarged view of the chorion. Figs 47–48, *C. bibioniformis*: 47, overall view; 48, enlarged view of the chorion.



Figs 49–57, *euceraeformis*-group: egg structure. Figs 49–51, *C. euceraeformis*: 49, overall view; 50, rosette; 51, enlarged view of the chorion. Figs 52–54, *C. leucopsiformis*: 52, overall view; 53, rosette; 54, enlarged view of the chorion. Figs 55–57, *C. crassicornis*: 55, overall view; 56, rosette; 57, enlarged view of the chorion.

Laboratory rearing. Mating occurred in the morning, immediately after eclosion. Females laid 151 eggs on average (range 140–168, n=5). Potential fecundity was 262 eggs (range 230–282, n=5).

Chamaesphecia leucopsiformis (Esper)

(figs 24–26, 37, 52–54)

Sphinx leucopsiformis Esper, 1800: 25.

Diagnosis. Alar expanse 12–21 mm. Fore wing in male pale brown-yellowish with all three hyaline areas well developed, ETA oval, divided into 3 cells. Apical area with white spots between the veins. Abdomen pale brown with distal margin of 4th tergite white bordered. Female similar to male, with reduced hyaline areas of fore wing and black-brown ground colour. The male and female genitalia are represented in figs 24–26, 37.

Egg structure. Eggs brown to dark brown ($0.83 \pm 0.01 \times 0.59 \pm 0.02$ mm, n=30), micropylar end broadly flattened, rosette and micropyle clearly visible (figs 52–54). Average number of aeropyles 21.3 ± 7.7 (n=15, range 7–42).

Distribution and habitat. Europe, but rare in Central Europe. Prefers sandy and coarse dry, well-exposed habitats.

Bionomics. Species univoltine. The host-plant is *E. cyparissias*. The flight period extends from the end of August to the beginning of October. *Chamaesphecia leucopsiformis* is the only *Chamaesphecia* species which flies in the autumn. Females oviposit on the stems of young plants or more rarely on the lower leaf surface. Young larvae walk down the stem and penetrate into the plant at the root-crown level or through the buds of new shoots. Larvae overwinter in the root. Larval development resumes in spring. The final instar is reached in early summer when the larvae enter summer aestivation. *Chamaesphecia leucopsiformis* and *C. empiformis* are sympatric species but their different phenologies prevent any major competition. Plants infested by *C. leucopsiformis* are either dry when *C. empiformis* oviposits or do not provide the secondary vegetative shoots that are needed by the latter species. The younger plants which will be selected by *C. leucopsiformis* in autumn are not attractive to *C. empiformis* in late spring–early summer of the following year.

Laboratory rearing. Copulation occurred in the late morning, immediately after emergence. Females laid 67 eggs on average (range 36–98, n=5). Potential fecundity was 128 eggs (range 76–169, n=5).

Chamaesphecia crassicornis Bartel

(figs 27–29, 38, 55–57)

Chamaesphecia crassicornis Bartel, 1912: 409.

Diagnosis. Alar expanse 16–22 mm. Fore wing of male dark brown with all hyaline areas well developed. Discal spot dark brown to black, ETA elongated oval, divided into 3–4 cells. Apical area brown, with golden-yellow spots between veins. Abdomen dark brown, posterior margins of 2nd, 4th and 6th (sometimes also 7th) tergite white bordered, with pale brown broken line medially. Anal tuft brown, externally and in the middle whitish-brown. Female similar to male, fore wing with less distinct hyline areas. The male and female genitalia are represented in figs 27–29, 38.

Egg structure. Eggs brown to dark brown, pear-shaped, with a pruinose surface ($0.91 \pm 0.02 \times 0.67 \pm 0.01$ mm, n=30), micropylar end narrower, crateriform, with short catkin-like protrusions, so that the rosette is open and visible at the bottom of the crater (figs 55–57). Average number of aeropyles 8.8 ± 2.0 (n=15, range 6–15).

Distribution and habitat. Eastern and south-eastern Europe. A rare species in Europe. Recorded in southern Russia, Kazakhstan and

Table 1. Leafy spurge suitability for eight European *Chamaesphecia* species.

Plant species	No. L1 transferred	Percentage survival	Larval instars (No.)
C. tenthrediniformis			
E. esula (s.s.) (Europe)	23	21.7	6th (5)
E. salicifolia	60	36.7	5th (1)/6th (21)
Leafy spurge			
– Saskatchewan	160	0	–
– Montana	20	0	–
E. virgata (Europe)	25	0	–
*C. empiformis**			
E. cyparissias	50	22.0	3rd–6th (11)
N.A. leafy spurge	50	0	–
*C. astatiformis***			
E. esula (s.s.) (Europe)	115	33.9	5th (3)/6th (36)
Leafy spurge			
– Saskatchewan	110	10.0	3rd (1)/4th (1)/5th (4)/6th (5)
– Montana	25	12.0	6th (3)
– Oregon	30	6.7	6th (2)
E. virgata (Europe)	69	2.9	5th (1)/6th (1)
*C. hungarica***			
E. lucida	225	22.7	3rd (2)/4th (15)/5th (11)/6th (14)/7th (9)
Leafy spurge			
– Saskatchewan	275	8.7	3rd (2)/4th (6)/5th (3)/6th (8)/7th (5)
– Montana	85	5.9	5th (2)/7th (3)
E. virgata (Europe)	25	8.0	3rd (1)/5th (1)
E. esula (s.s.) Europe	20	5.0	6th (1)
C. bibioniformis			
E. seguieriana	150	21.3	3rd (3)/4th (8)/5th (4)/6th (15)/7th (2)
Leafy spurge			
– Saskatchewan	154	0.6	5th (1)
– Montana	40	0	–
C. euceraeformis			
E. polychroma	45	28.9	6th (9)/7th (4)
Leafy spurge			
– Saskatchewan	30	0	–
– Montana	25	0	–
E. virgata (Europe)	20	0	–
C. palustris			
E. palustris	100	18.0	4th (5)/5th (9)/6th (4)
Leafy spurge			
– Saskatchewan	80	1.3	5th (1)
– Montana	20	0	–
*C. crassicornis****			
E. virgata (Europe)	27	33.3	2nd (3)/3rd (3)/4th (3)
N.A. leafy spurge	18	27.8	2nd (5)

*Data from Schroeder (1969); **data from Gassmann & Tosevski (1994); ***data from Gassmann (1994).

Kirgizia. Mainly along roads and embankments, in dry to mesic-dry loamy habitats, also on poorer soils where spurge is intermixed with a dense and high vegetation.

Bionomics. The host-plant is *E. virgata*. The adults fly in July. Eggs are laid singly on the stem or in the leaf axil. Neonate larvae drop to the ground and bore directly into the root. In spring, larvae bore into the central part of the root where development continues. The larvae, which have an annual or biennial development, pupate in early June on the top of the exit tunnel. There is no cocoon.

Laboratory rearing. Copulation occurred late in the morning, 1–4 days after the eclosion. Mated females laid on average 80 eggs (range 15–146; n=9). Potential fecundity was 163 eggs (range 83–178).

Suitability of leafy spurge for *Chamaesphecia* spp.

The larvae of only three of the eight *Chamaesphecia* spp. investigated feed and develop in the roots of North American leafy spurge (table 1). Of these, the best candidate is *C. crassicornis* the larvae of which had a similar survival rate on North American leafy spurge and the European *E. virgata*. Larval development was slightly delayed on the target weed because of delayed larval transfer during summer. *Chamaesphecia astatiformis* and *C. hungarica* each had a lower larval survival rate on the target weed than on their European host, and thus are suboptimal candidates for the biological control of leafy spurge. The very low rate of larval survival on the target weed of *C. bibioniformis* and *C. palustris* excludes their establishment on leafy spurge in North America. The larvae of *C. tenthrediniformis* did not accept leafy spurge from Saskatchewan and Montana as host-plants, and no larval development occurred on European *E. virgata* either. Our data confirm that leafy spurge is not a suitable host-plant for this species (Harris, 1984).

Discussion

Based on the morphology of male genitalia, the ten *Chamaesphecia* spp. which develop on *Euphorbia* in Europe, can be divided into two groups: the *tenthrediniformis*-group and the *euceraeformis*-group. *Chamaesphecia tenthrediniformis, C. empiformis, C. astatiformis, C. hungarica, C. bibioniformis* and *C. myrsinites* belong to the *tenthrediniformis*-group. They are morphologically closely related, with characteristic bands on the 2nd, 4th and 6th (for males also 7th) abdominal tergites and with similar colour patterns. The dorso-basal part of the valvae in the male genitalia is characterized by specialized setae which are robust and strongly hooked at the tip (figs 3, 4). *Chamaesphecia euceraeformis, C. palustris, C. leucopsiformis* and *C. crassicornis* belong to the *euceraeformis*-group. They are morphologically well differentiated species, mostly with a clearly designated white band on the 4th abdominal tergite. The group of strongly hooked setae is absent on the dorso-basal part of the valvae in the male genitalia (figs 19, 20). With the exception of *C. astatiformis*, the average number of aeropyles in the central part of the egg chorion is higher for the *tenthrediniformis*-group of species than for the *euceraeformis*-group of species. With regard to the egg chorion structure, *C. astatiformis* is closely related to species in the *euceraeformis*-group, while *C. crassicornis* is closely related to the *tenthrediniformis*-group by its external morphological characteristics. Note that the egg chorion of both species is characterized by a crater-shaped micropylar end and by more or less visible protrusions hiding the rosette.

The intraspecific variability in the morphology (Radcliff-Smith, 1985; Harvey *et al.*, 1988) and chemistry (Evans *et al.*, 1991; Holden & Mahlberg, 1992) of spurge populations is likely to be followed by an intraspecific variability of *Chamaesphecia* spp. as indicated by the phenological differences between populations of *C. tenthrediniformis* reared from two different host-plants (*E. esula* sensus stricto and *E. salicifolia*) which could represent the initial phase in speciation of its populations. Along with a differentiation in the host-plants and the flight periods, populations of *Chamaesphecia* spp. in Europe are closely tied to their habitats.

In Europe, most *Chamaesphecia* spp. attacking spurges are monophagous, with the exception of *C. tenthrediniformis* which develops in two closely related species, *E. esula* sensu stricto and *E. salicifolia*, and possibly *C. euceraeformis* which develops in *E. polychroma* and *E. austriaca*. The field host range of these two species would therefore suggest a higher potential for acceptance of North American leafy spurge. This assumption however could not be confirmed. Only three of the eight *Chamaesphecia* spp. investigated attacked and developed in leafy spurge, i.e. *C. hungarica, C. astatiformis* and *C. crassicornis*. *Chamaesphecia astatiformis* and *C. tenthrediniformis* originating from *E. esula* sensu stricto apparently have requirements which are not met by *E. virgata* and only partially met by leafy spurge. On the other hand, the larval survival rate of *C. crassicornis* reared from *E. virgata* was found to be similar on its European host and North American leafy spurge. Within the *E. esula* group of species, it is the moths reared from *E. esula* sensu stricto which have particular host-plant requirements with regard to North American leafy spurge. According to the requirements of *Chamaesphecia* spp., *E. virgata* is more closely related to North American leafy spurge than is *E. esula* sensu stricto, and *C. crassicornis* appears to be the best candidate for the biological control of leafy spurge in North America.

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